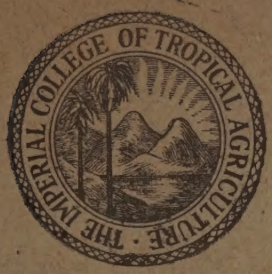

Via colendi haud facilis

DEPARTMENT OF MYCOLOGY AND BACTERIOLOGY

MEMOIR No. 8.—STUDIES IN THE WITCHES' BROOM DISEASE OF CACAO CAUSED BY *MARASMIUS PERNICIOSUS* STAHEL.

PART II.—FIELD STUDIES AND CONTROL METHODS

BY

R. E. D. BAKER AND S. H. CROWDY

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TRINIDAD, B.W.I.

JANUARY, 1944.

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STUDIES IN WITCHES' BROOM DISEASE OF CACAO CAUSED BY *MARASMIUS PERNICIOSUS* STAHEL

FIELD STUDIES AND CONTROL METHODS

BY

R. E. D. BAKER AND S. H. CROWDY

I.—Introduction

In the first memoir of this series Baker and Crowdy (3) discussed the life history, symptoms, morphology and etiology of witches' broom disease, and some observations on the resistance of certain Imperial College selections of cacao to the disease were recently published by the same authors (2). The work of the Trinidad Department of Agriculture on this disease was summarised by Baker, Crowdy and Thorold (4) in 1941 and the results of three years work at River Estate have been outlined by Baker (1). The object of this second memoir is to discuss observations made in the field at River Estate and elsewhere and to present a full account of our knowledge of control methods in the light of recent research.

From September 1939 to September 1942 a plot of 76 trees at River Estate, Diego Martin, Trinidad, was kept under observation. The trees were eight years old at the beginning of the experiment, 12 feet apart with sparse immortel shade. These trees represent the open pollinated seedling progeny of I.C.S.1 and can be taken as representative of a good type of Trinidad 'seedling' cacao. Observations have also been made on much younger clonal material of Imperial College selections in an adjoining field.

The disease has become rapidly worse in this plot during the course of the investigation (Table I). For some years prior to 1938 a few brooms had been noticed, but in 1938 the disease for the first time began to assume serious proportions at River Estate. In 1939 it became evident that this estate with its large area of well-kept cacao trees whose history was known, had become an ideal locality for the study of witches' broom disease and the present series of investigations was started. By the end of 1942 the disease had become exceedingly serious, and it has been possible to study its development from a light attack in early 1939

to what is probably its maximum intensity in late 1942. Its rapid development is best illustrated by the increase in fan brooms, of which under 2,000 were removed in 1939-40, about 6,000 in 1940-41 and over 10,000 in 1941-42 from the 76 trees under investigation (Table I).

TABLE I

Brooms removed 1939 to 1942

	1939-40	1940-41	1941-42
Total brooms	3,901	12,321	15,612
Mean per tree	51	162	205
Fan and *chupon brooms only ...	1,793	5,616	10,253
Mean per tree	23	74	135
Cushion brooms only	2,108	6,705	5,359
Mean per tree	28	88	70

* Chupon brooms are rare and represent less than 1 per cent. of the total.

In the main experiment brooms were removed every two weeks and classified according to the system previously outlined (3). At the same time observations were made on the flowering, flushing, yield and general condition of the trees, and records were kept of rainfall, humidity and temperature by means of recording instruments. Other observations, such as height above ground, position on the tree and size of brooms were kept for a time.

Brooms were removed from the adjoining clonal plots of I.C. selections once a month at first, but later, for a comparison of resistance only, this was found to be unnecessary and they were removed twice a year, in November and again in March after their period of maximum occurrence.

Both leaf flush and intensity of flowering were estimated once a week by the method of awarding marks from 0 to 5 ; 0 for no flowers or flush and 5 for the maximum possible amount it was considered that any tree in the plot could carry.

II.—Individual Tree Data

The different types of broom have been described and illustrated already (3) and their relative abundance is shown in Table II. The clonal material shows a higher percentage of fan and chupon brooms because it is younger and has not come into full bearing, and also a higher percentage of most of the larger types of broom (A3, B2, B3, and C2). This is partly due to the vigour of the younger trees and partly to the fact that on the younger trees brooms were cut once a month instead of every two weeks and therefore had a longer time in which to develop.

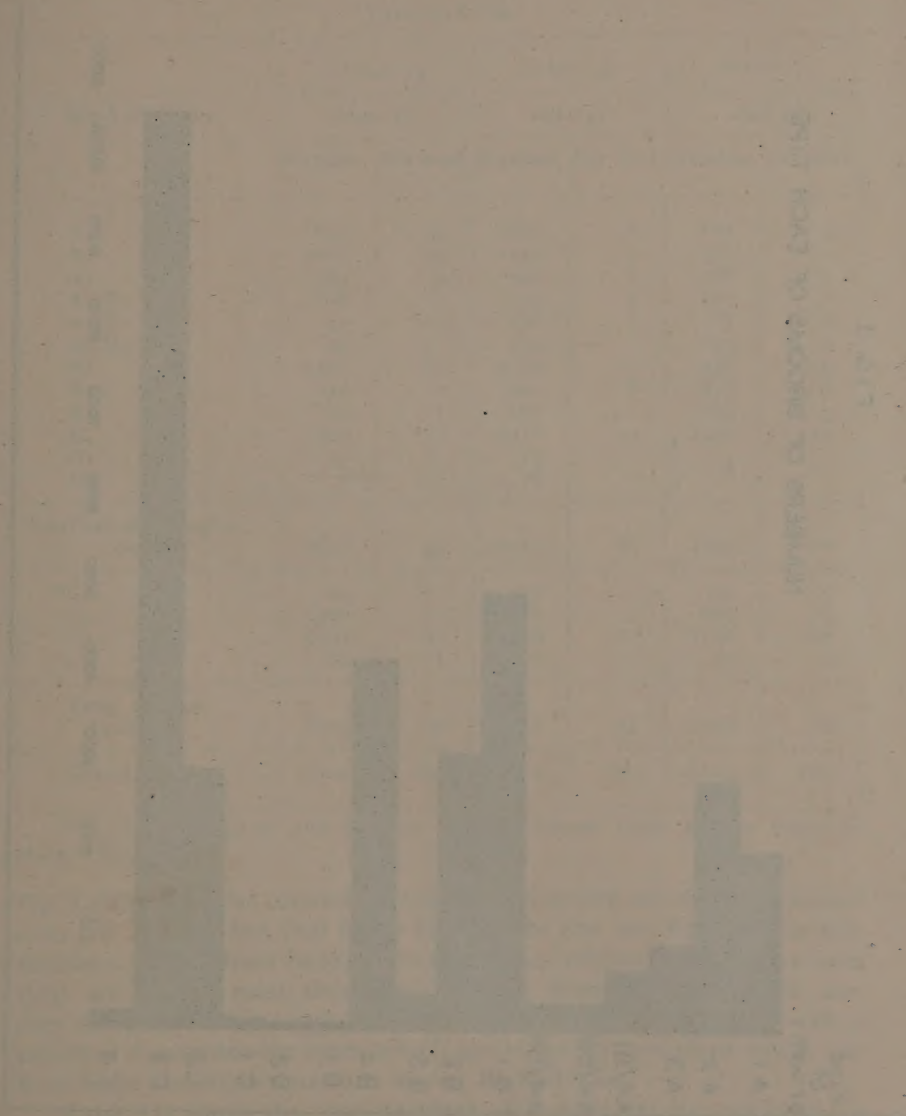


FIG. I.

NUMBERS OF BROOMS OF EACH TYPE

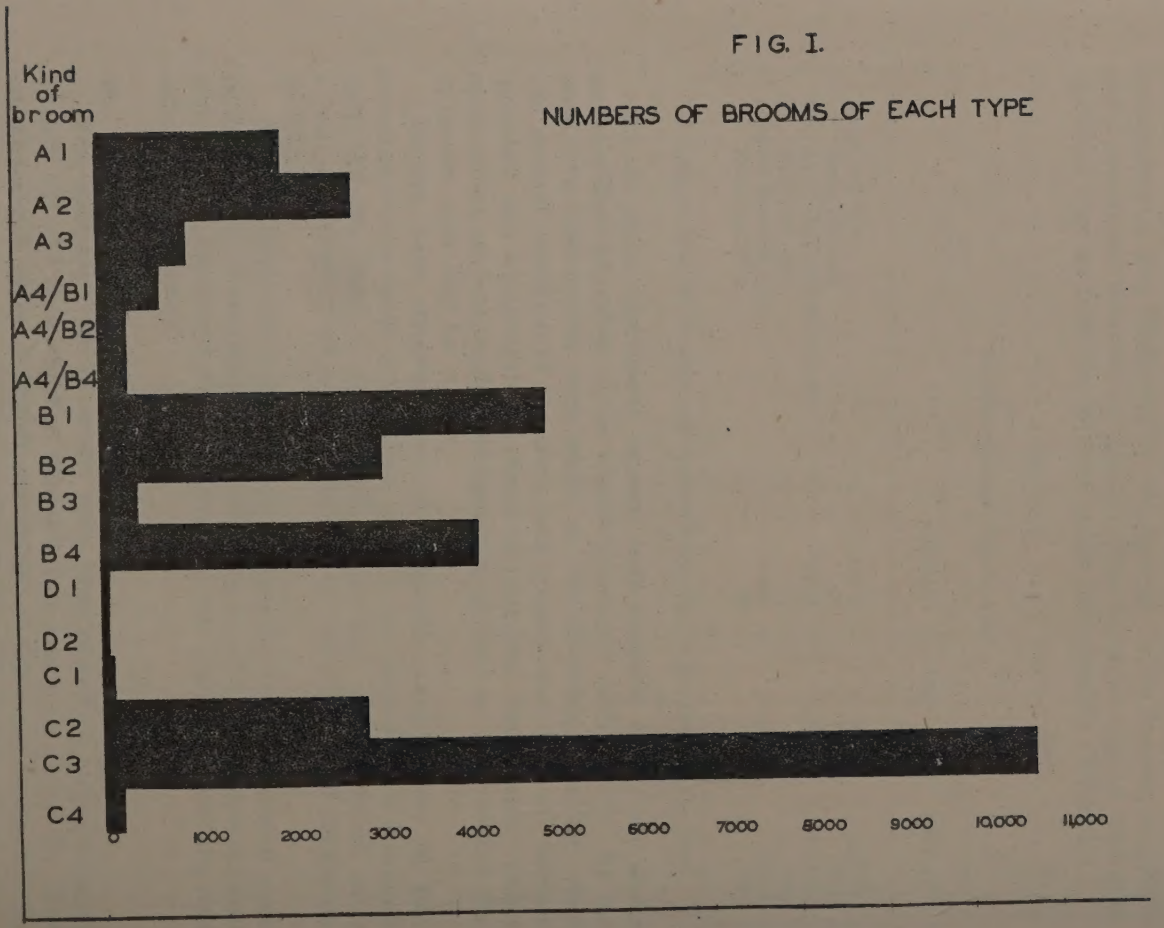


TABLE II

Types of broom

Kind of broom	Field 19 1940-41		Field 19 1941-42		Field 7 1941-42	
	Number	Per cent.	Number	Per cent.	Number	Per cent.
A1	633	5	1267	8	181	3
A2	1067	9	1454	9	375	6
A3	363	3	442	3	228	3
A4/B1	128	1	433	3	120	2
A4/B2	47	—	136	1	87	1
A4/B4	29	—	134	1	115	2
B1	1485	12	2722	17	938	14
B2	912	7	1240	8	1076	16
B3	66	1	102	1	255	4
B4	860	7	2278	15	1210	19
D1	20	—	19	—	4	—
D2	6	—	26	—		
Total fan and chupon brooms ...	5616	45	10253	66	4589	70
*C1	24	—	19	—	32	—
C2	1326	11	1016	7	689	11
C3	5295	43	4276	27	1148	18
C4	60	1	48	—	57	1
Total cushion brooms ...	6705	55	5359	34	1926	30
Grand total ...	12321	100	15612	100	6515	100

*The illustrations of and the key to these broom types will be found in Memoir No. 7.

Fig. I shows that the commonest types of fan broom are the small lateral ones (B1 and B4) but that larger fan brooms (A2 and B2) occur in fair numbers. Of cushion brooms the small ones without vegetative shoots (C3) are far the most abundant. Chupon brooms (D1 and D2) are rare as chupons are normally removed at regular intervals. From a practical standpoint the types which are important are those which are both large and numerous such as A2, B2 and C2.

Table III shows the total numbers of brooms per tree which have been removed during the three years of the experiment. Several points are noteworthy, firstly, the variation from tree to tree, the extreme range in 1941-42 being from 14 brooms recorded on tree 37 to 594 on tree 28. Secondly, there are positive correlations ($r = +0.77^{**}$ and $+0.73^{**}$) between the first and second and second and third years results—it can

TABLE III

Total brooms—September, 1939 to September, 1942

Tree No.	Total brooms 1939-40	Total brooms 1940-41	Total brooms 1941-42	Tree No.	Total brooms 1939-40	Total brooms 1940-41	Total brooms 1941-42
1 ...	55	285	397	40 ...	7	105	239
2 ...	19	37	120	41 ...	13	49	88
3 ...	22	91	124	42 ...	10	45	79
4 ...	25	109	138	43 ...	5	19	41
5 ...	38	103	122	44 ...	2	11	27
6 ...	18	88	161	45 ...	9	48	99
7 ...	10	46	95	46 ...	24	152	150
8 ...	101	324	377	47 ...	42	165	160
9 ...	58	211	270	48 ...	178	553	458
10 ...	113	269	316	49 ...	69	181	197
11 ...	51	154	238	50 ...	222	1015	391
12 ...	123	248	287	51 ...	57	156	104
13 ...	292	279	345	52 ...	12	52	99
14 ...	73	141	227	53 ...	9	55	101
15 ...	66	154	345	54 ...	35	78	173
16 ...	22	71	134	55 ...	28	213	256
17 ...	15	48	107	56 ...	33	116	150
18 ...	59	214	469	57 ...	51	170	228
20 ...	45	150	314	58 ...	21	50	142
21 ...	75	188	257	59 ...	14	82	98
22 ...	19	74	72	60 ...	11	104	201
23 ...	7	14	44	61 ...	26	33	96
24 ...	148	321	304	62 ...	33	301	336
25 ...	36	84	198	63 ...	41	216	292
26 ...	15	40	119	64 ...	144	388	505
27 ...	62	202	181	65 ...	43	401	266
28 ...	124	290	594	66 ...	67	303	421
29 ...	135	299	205	67 ...	45	204	234
30 ...	23	75	184	68 ...	48	282	418
31 ...	92	161	194	69 ...	149	285	532
32 ...	24	83	101	70 ...	12	72	78
33 ...	95	244	322	71 ...	24	92	174
34 ...	20	31	51	72 ...	35	108	148
35 ...	94	310	267	73 ...	4	44	60
36 ...	51	67	106	74 ...	16	54	110
37 ...	5	30	14	75 ...	17	60	110
38 ...	39	159	167	76 ...	3	40	57
39 ...	64	231	228	77 ...	9	63	100

Total—1939-40 3,901
1940-1941... 12,321
1941-42 15,612

Correlation, that trees producing many brooms in the one year did so again in the next year.

1939-40 and 1940-41 r=0.77
1940-41 and 1941-42 0.73

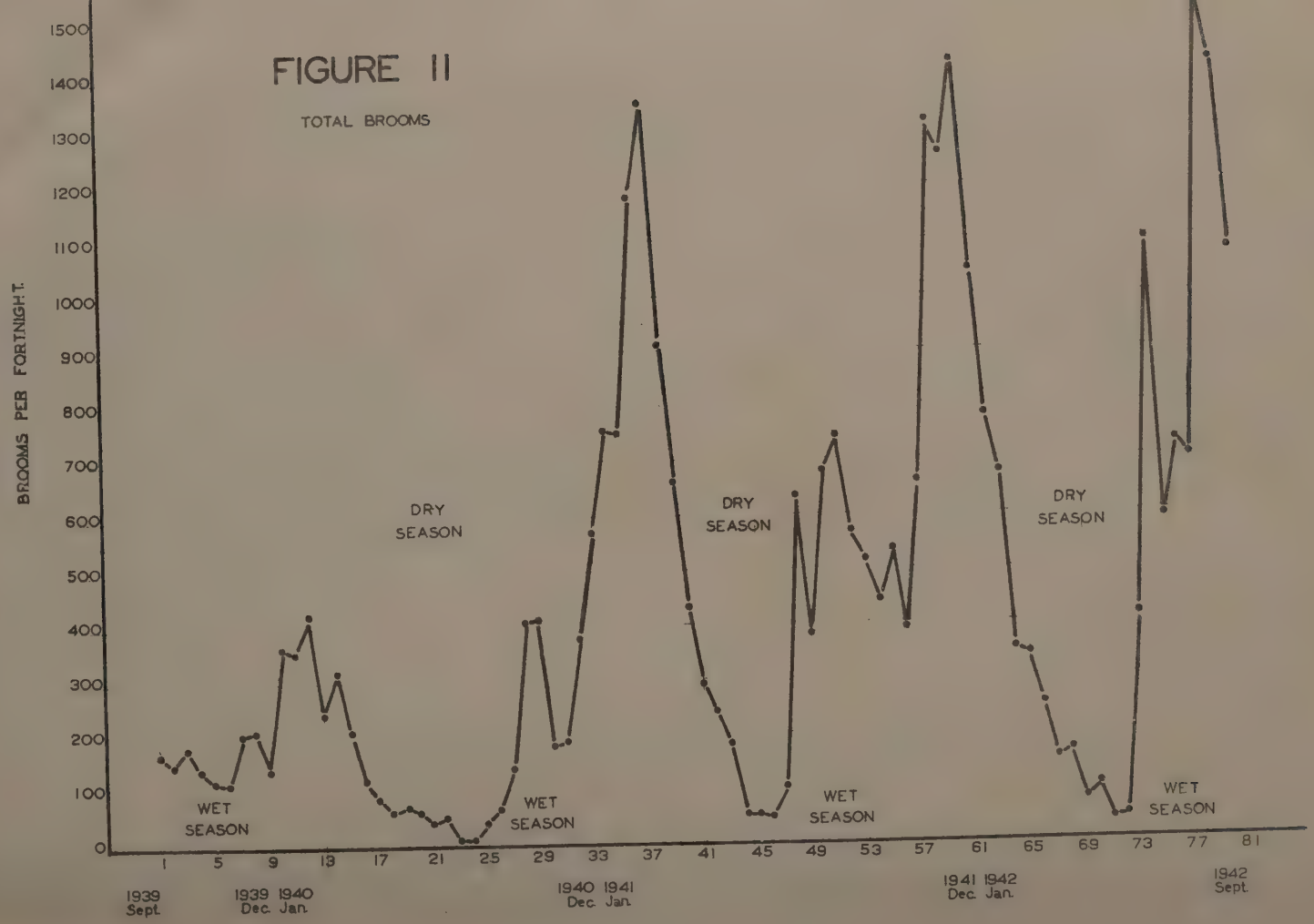


FIGURE 11
TOTAL BROOMS
BROOMS PER FORTNIGHT.
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1 5 9 13 17 21 25 29 33 37 41 45 49 53 57 61 65 69 73 77 81
1939 Sept.
1939 1940 Dec. Jan.
1940 1941 Dec. Jan.
1941 1942 Dec. Jan.
1942 Sept.
WET SEASON
DRY SEASON
WET SEASON
DRY SEASON
WET SEASON
DRY SEASON
WET SEASON

therefore be taken as an established fact that trees which produce many brooms one year are likely to do so again the next year, and that trees which produce only a few brooms one year are likely to behave similarly in the following year. This relationship naturally tends to disappear when trees are so badly attacked as to be seriously damaged either directly or by the removal of brooms. Thirdly, several trees (*e.g.* Nos. 27, 29, 35, 39, 48, 50 and 65) produced fewer brooms in 1941-42 than they did in 1940-41 although the total for the plot increased from 12321 to 15612, suggesting that these trees, which are amongst those which produced most brooms in 1940-41, have already begun to suffer from the cumulative effects of the disease. Certain trees such as No. 1, which are exceptionally large and vigorous, have produced many brooms each year without any noticeable loss of vigour. The way in which the disease has become steadily worse in this plot is indicated in Figure II showing the fortnightly totals of brooms removed from 1939 to 1942.

Tables IV and V show fan brooms and cushion brooms analysed separately. The separation of brooms into two groups in this way makes an appreciable difference to the year-to-year correlation coefficients, fan brooms per tree showing a higher positive correlation ($r = +0.082^{**}$ and $+0.87^{**}$) than cushion brooms ($r = +0.76^{**}$ and $+0.58^{**}$) for the three years of the experiment. Table V shows that the tree to tree variation for cushion brooms is much greater than for fan brooms as certain trees such as Nos. 13, 18, 24, 48, 50, 63, 64 and 66 produce relatively enormous numbers of the C2 and C3 type of brooms. The lower correlation coefficient for cushion brooms between 1940-41 and 1941-42 is caused by the partial cessation of flowering by certain heavily diseased trees (*e.g.* Nos. 13, 24, 48, 50 and 65).

The direct correlation between fan brooms per tree and cushion brooms per tree ($r = +0.30^{**}$ and $+0.34^{**}$) is low in the data for the first two years only and is lower still ($r = +0.14$) for the third year. This indicates that if there is any inherent relationship between the two it is masked by other factors, of which the most important is probably the time for which the cushions remain active (and presumably open to infection) during the year. Size of cushion will also be important as spores are more likely to be caught by a large cushion with many buds than by a smaller one. Some indication of this can be obtained from the intensity of flower production of the trees which was estimated weekly during the second and third years of the investigation. The intensity of flowering during the year for any tree in the plot was found to be strongly correlated with the number of cushion brooms it produced during the year (1940-41 $r = +0.57,^{**}$ 1941-42 $r = +0.77^{**}$). It was therefore expected that if partial correlations were calculated, and the

TABLE IV

Fan and Chupon brooms—September, 1939 to September, 1942

Tree No.	Fan and chupon brooms			Tree No.	Fan and chupon brooms		
	1939-40	1940-41	1941-42		1939-40	1940-41	1941-42
1 ...	41	150	290	40 ...	5	38	74
2 ...	16	25	82	41 ...	8	32	68
3 ...	18	70	120	42 ...	7	34	77
4 ...	20	86	115	43 ...	4	10	25
5 ...	15	66	113	44 ...	2	11	27
6 ...	18	74	152	45 ...	7	27	86
7 ...	7	38	74	46 ...	18	84	123
8 ...	49	151	189	47 ...	12	28	97
9 ...	50	179	245	48 ...	16	53	108
10 ...	33	79	143	49 ...	38	109	160
11 ...	32	84	200	50 ...	47	270	356
12 ...	82	155	240	51 ...	28	79	92
13 ...	25	64	127	52 ...	6	26	83
14 ...	46	106	195	53 ...	4	39	68
15 ...	47	117	309	54 ...	10	48	106
16 ...	14	44	110	55 ...	18	153	202
17 ...	10	33	50	56 ...	11	54	120
18 ...	11	45	76	57 ...	48	141	192
20 ...	37	84	208	58 ...	15	31	114
21 ...	54	128	184	59 ...	5	40	55
22 ...	18	39	62	60 ...	5	54	129
23 ...	7	14	44	61 ...	22	22	59
24 ...	35	22	140	62 ...	12	94	191
25 ...	31	67	174	63 ...	4	20	53
26 ...	12	29	81	64 ...	27	114	97
27 ...	38	73	104	65 ...	11	74	146
28 ...	61	144	388	66 ...	16	36	145
29 ...	30	88	113	67 ...	35	132	216
30 ...	15	51	166	68 ...	31	137	314
31 ...	33	89	147	69 ...	74	175	290
32 ...	16	66	89	70 ...	10	26	62
33 ...	64	172	300	71 ...	18	64	143
34 ...	20	22	47	72 ...	25	81	127
35 ...	64	182	231	73 ...	4	33	59
36 ...	23	52	96	74 ...	12	30	90
37 ...	2	24	14	75 ...	16	56	99
38 ...	22	83	149	76 ...	3	15	44
39 ...	34	77	104	77 ...	9	61	85

Total—1939-40	... ...	1,793
1940-41	... ...	5,603
1941-42	... ...	10,253

Correlation, that trees producing many Fan and Chupon brooms in the one year did so again in the next year

1939-40 and 1940-41	r=0.82
1940-41 and 1941-42	0.87

TABLE V

Cushion Brooms—September, 1939 to September, 1942

Tree No.	Cushion brooms			Tree No.	Cushion brooms		
	1939-40	1940-41	1941-42		1939-40	1940-41	1941-42
1 ...	14	135	107	40 ...	2	67	165
2 ...	3	12	38	41 ...	5	17	20
3 ...	4	21	4	42 ...	3	11	2
4 ...	5	23	23	43 ...	1	9	16
5 ...	23	37	9	44 ...	0	0	0
6 ...	0	14	9	45 ...	2	21	13
7 ...	3	8	21	46 ...	6	68	27
8 ...	52	173	188	47 ...	30	137	63
9 ...	8	32	25	48 ...	162	500	350
10 ...	80	190	173	49 ...	31	72	37
11 ...	19	70	38	50 ...	175	745	35
12 ...	41	93	47	51 ...	29	77	12
13 ...	267	215	218	52 ...	6	26	16
14 ...	27	35	32	53 ...	5	16	33
15 ...	19	37	36	54 ...	25	30	67
16 ...	8	27	24	55 ...	10	60	54
17 ...	5	15	57	56 ...	22	62	30
18 ...	48	169	393	57 ...	3	29	36
20 ...	8	66	106	58 ...	6	19	28
21 ...	21	60	73	59 ...	9	42	43
22 ...	1	35	10	60 ...	6	50	72
23 ...	0	0	0	61 ...	4	12	37
24 ...	113	299	164	62 ...	21	207	145
25 ...	5	17	24	63 ...	37	196	239
26 ...	3	11	38	64 ...	117	274	408
27 ...	24	129	77	65 ...	32	327	120
28 ...	63	146	206	66 ...	51	267	276
29 ...	105	211	92	67 ...	10	72	18
30 ...	8	24	18	68 ...	17	145	104
31 ...	59	72	47	69 ...	75	110	242
32 ...	8	17	12	70 ...	2	46	16
33 ...	31	72	22	71 ...	6	28	31
34 ...	0	9	4	72 ...	10	27	21
35 ...	30	128	36	73 ...	0	11	1
36 ...	28	15	10	74 ...	4	24	20
37 ...	3	6	0	75 ...	1	4	11
38 ...	17	76	18	76 ...	0	25	13
39 ...	30	154	124	77 ...	0	2	15

Total—1939-40 2,108
1940-41 6,688
1941-42 5,359

Correlation, that trees producing many Cushion brooms in the one year did so again in the next year
1939-40 and 1940-41 r=0.76
1940-41 and 1941-42 0.58

effect of the intensity of flowering thus eliminated, the correlations between fan brooms and cushion brooms per tree would be improved. However no very strong partial correlations were found (1939-40 r= +0.39**, 1940-41 r= +0.51**, 1941-42 r= +0.17) which would seem to suggest that other important factors were operating.

It was also considered likely that, since only young developing tissues can be infected by the disease, the trees which 'flushed' most during the year would produce the largest number of fan brooms. Contrary to expectation this was not found to be the case : for very low correlation coefficients (in 1940-41 r= +0.05) were found between an estimation of the total flush per tree and the number of fan brooms produced per tree. In 1941-42 a low but just significant positive correlation (r= +0.22*) was obtained. This correlation was not appreciably improved by eliminating the dry season flushes which occurred at a time when no infection was possible. Brooms do nevertheless tend to appear with the 'flush' or slightly before it (Fig. V) and there is a slight positive correlation (r= +0.31**) between the total flush figure for the plot for any week and the number of fan brooms collected during the same week.

The absence of substantial positive correlation between total flush and total fan brooms per tree per year was quite unexpected and suggests that there are other very important factors besides flush affecting the variation in number of fan brooms from tree to tree, and it is reasonable to assume that the most important of these factors are likely to be differences in susceptibility to the production of such brooms. Nevertheless the strong positive correlation between the number of flowers produced and the number of cushion brooms per tree per year suggests that this resistance can hardly be physiological but more likely some form of disease avoidance on the part of the vegetative buds of certain trees. This is supported by the fact that fan broom and cushion broom production per tree are not closely correlated, as would be expected if the mechanism of resistance was physiological†. In addition the brooms produced on the supposedly resistant trees are of normal appearance—they are not small or poorly developed as might be expected on a tree with physiological resistance, but are just as large as those occurring on the most susceptible trees. It therefore does not follow that a tree which shows resistance to fan brooms will show any comparable resistance to cushion brooms or to pod infection. Conversely, a tree severely attacked by fan brooms and cushion brooms might produce pods which, by reason of some character of the pod such

† In this paper the term 'morphological resistance' is taken to mean resistance associated with some morphological character such as hairy bud-scales, thick cuticle or closely folded stipules ; while 'physiological resistance' means resistance due to an inherent property of the plant cell.

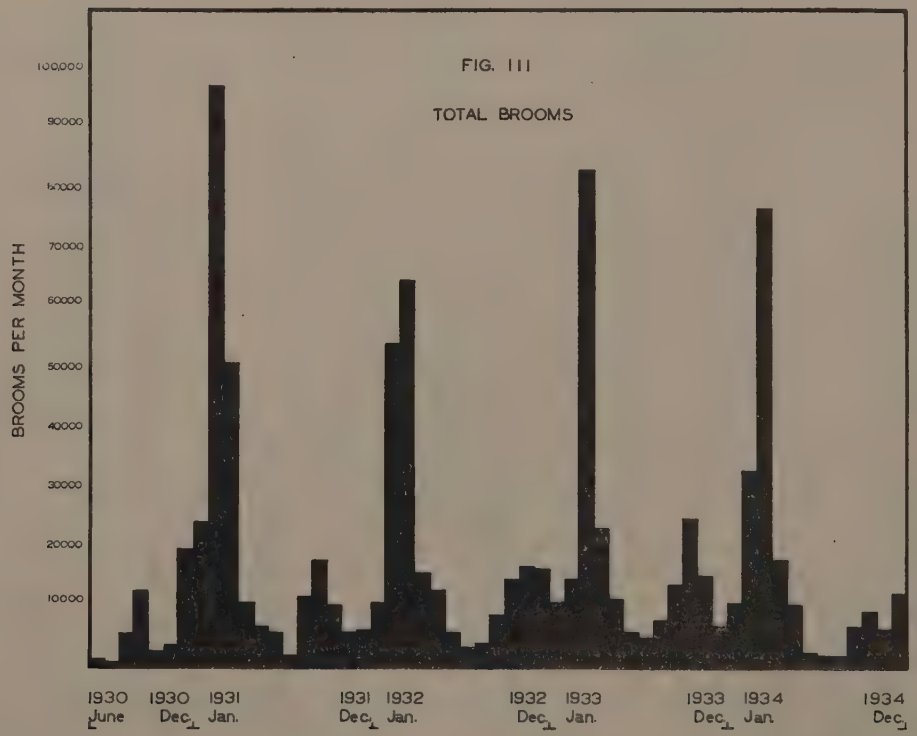


FIG. 111
TOTAL BROOMS
BROOMS PER MONTH
100000
90000
80000
70000
60000
50000
40000
30000
20000
10000
1930 June
1930 Dec.
1931 Jan.
1931 Dec.
1932 Jan.
1932 Dec.
1933 Jan.
1933 Dec.
1934 Jan.
1934 Dec.

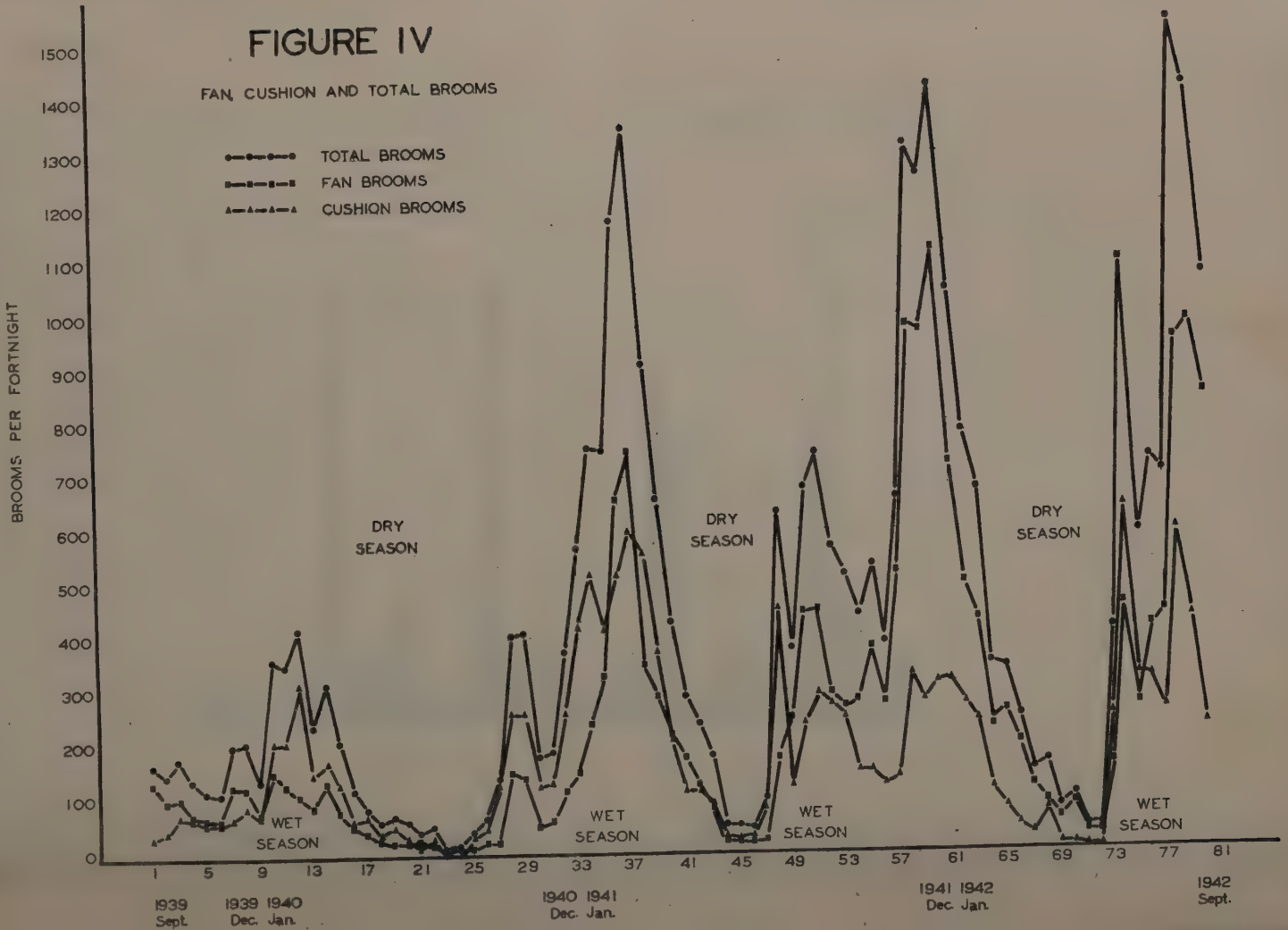


FIGURE IV
FAN, CUSHION AND TOTAL BROOMS
TOTAL BROOMS
FAN BROOMS
CUSHION BROOMS
BROOMS PER FORTNIGHT
1500
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
DRY SEASON
DRY SEASON
DRY SEASON
WET SEASON
WET SEASON
WET SEASON
WET SEASON
1 5 9 13 17 21 25 29 33 37 41 45 49 53 57 61 65 69 73 77 81
1939 Sept.
1939 1940 Dec. Jan.
1940 1941 Dec. Jan.
1941 1942 Dec. Jan.
1942 Sept.

as a very smooth or waxy surface, might show resistance to the disease. No. 18 is an example of a tree which produces comparatively few fan brooms but is free-flowering and therefore heavily attacked by cushion brooms. There is as yet little data on the subject of pod resistance, but the available evidence does not indicate that trees showing resistance to fan brooms show any comparable resistance in their pods. In the control of the disease, resistance to fan brooms might be much more important than pod resistance, as trees with susceptible vegetative tissues would always be seriously damaged by the disease while trees which showed resistance to fan brooms would be healthy. Furthermore if planted in large blocks, trees resistant to fan brooms might carry healthy pods as these would escape infection even though they were susceptible.

III. –Seasonal Variation

The existence of a marked seasonal variation in the number of brooms produced on cacao trees has been realised for some time and was discussed by Baker, Crowdy and Thorold (4) in 1941. Figure III reproduced from this article and compiled from data collected at Marper Estate, Trinidad, from 1930 to 1934 by the Trinidad Department of Agriculture indicates a marked maximum in February or March followed by an equally pronounced minimum in June or July. From August to January the number fluctuates about an intermediate value.

In 1939 more detailed experiments were set up at River Estate to find out the reason for this seasonal variation. From what is already known about the life history of the disease (3) it is clear that certain conditions have to be fulfilled before infection can occur. The most important of these are firstly, an adequate supply of viable spores ; secondly, buds, cushions or pods of a suitable age–results of inoculation experiments indicate that only very young developing tissues can be infected ; and thirdly, favourable environmental and climatic factors. These latter, which have so far not been fully investigated, are undoubtedly of great importance.

At River Estate brooms were removed fortnightly instead of at monthly intervals as had been done at Marper Estate. Figure IV shows fortnightly totals of fan brooms, cushion brooms and total brooms for River Estate. It agrees closely with the Marper Estate results in showing a marked maximum about January, followed by a minimum in June or July, and as at Marper there is a period from August to December when the values fluctuate. If fan brooms alone are considered it will be seen that in addition to the marked maximum and minimum in January and June there are secondary maxima and minima three or four times a year. Figure V shows fan brooms per fortnight and flush per fortnight plotted together. The rough similarity of the graphs and

the positive correlation ($r = +0.31^{**}$) indicate that flushing, and therefore the presence of developing vegetative buds on the trees has some effect on the incidence of the disease. Figure VI shows similar graphs for cushion brooms and flowers and here again the indication is that an increase in flowering is followed about five weeks later by an increase in cushion broom formation. Fan brooms will of course be expected to develop *with the flush*, but cushion brooms will appear some time *after* the increase in flowering was noticed. Although a rough parallelism can be seen in both Figures V and VI it is evident that other and more important factors are at work in controlling the seasonal incidence of the disease.

In Figure VII the total number of brooms produced per fortnight is compared with the sporophore index† and here again there is undoubted similarity. Shortly before and during the period of maximum broom formation (December and January) the sporophore index is high ; similarly at the end of the dry season when broom formation is at a minimum the sporophore index is low ; and thirdly both in 1941 and 1942 the sharp increase in the sporophore index which occurs with the first rains of the wet season was followed some five weeks later by the first sharp rise in broom formation. In addition, there is a positive correlation ($r = +0.47^{**}$) for the sporophore index in any given week and the total number of brooms produced five weeks later. The fact that this correlation coefficient came out as high as 0.47 in spite of other factors operating which include intensity of flush, intensity of flowering, climatic factors and particularly the known variation in broom development after inoculation between extremes of three weeks and about three months (five weeks is merely an approximation to the modal period) seems to be a strong indication that the supply of spores is of considerable importance in this disease, even in heavily infested areas.

Only incomplete evidence of the effect of climatic and environmental factors is at present available, but relevant data indicate that it is a subject of major importance both in accounting for seasonal fluctuations in broom formation, and also for regional differences in the intensity of the disease. It has already been shown (3) that weather and climatic factors play an important part in sporophore production, and it is of course possible that environmental conditions favourable for sporophore production are identical with those necessary for infection, which would accentuate any correlation between brooms and sporophores. A study of environmental and climatic factors will be a logical corollary to these investigations.

†The number of sporophores per week produced by a random sample of one hundred brooms of all kinds.

FIGURE V

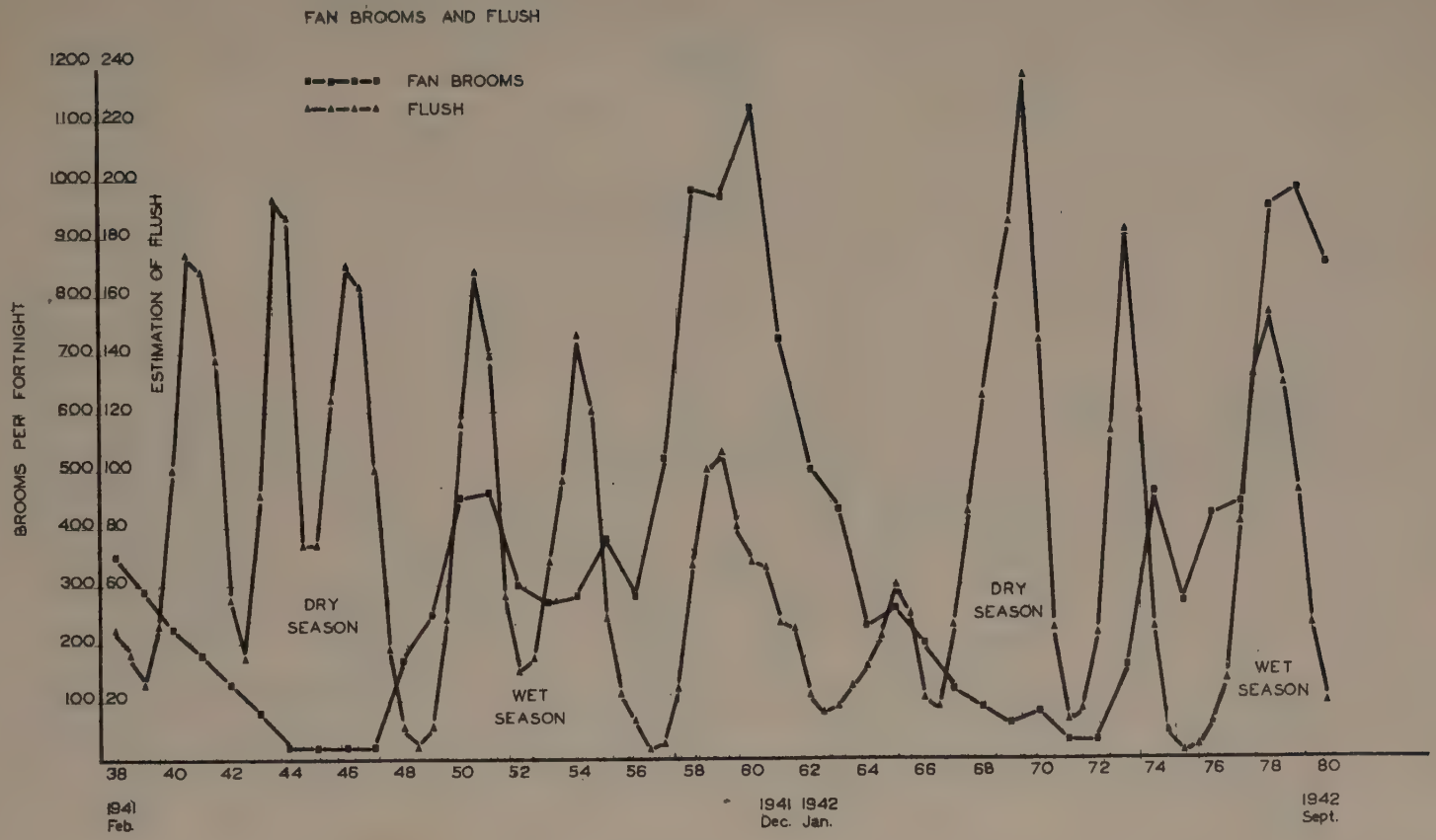
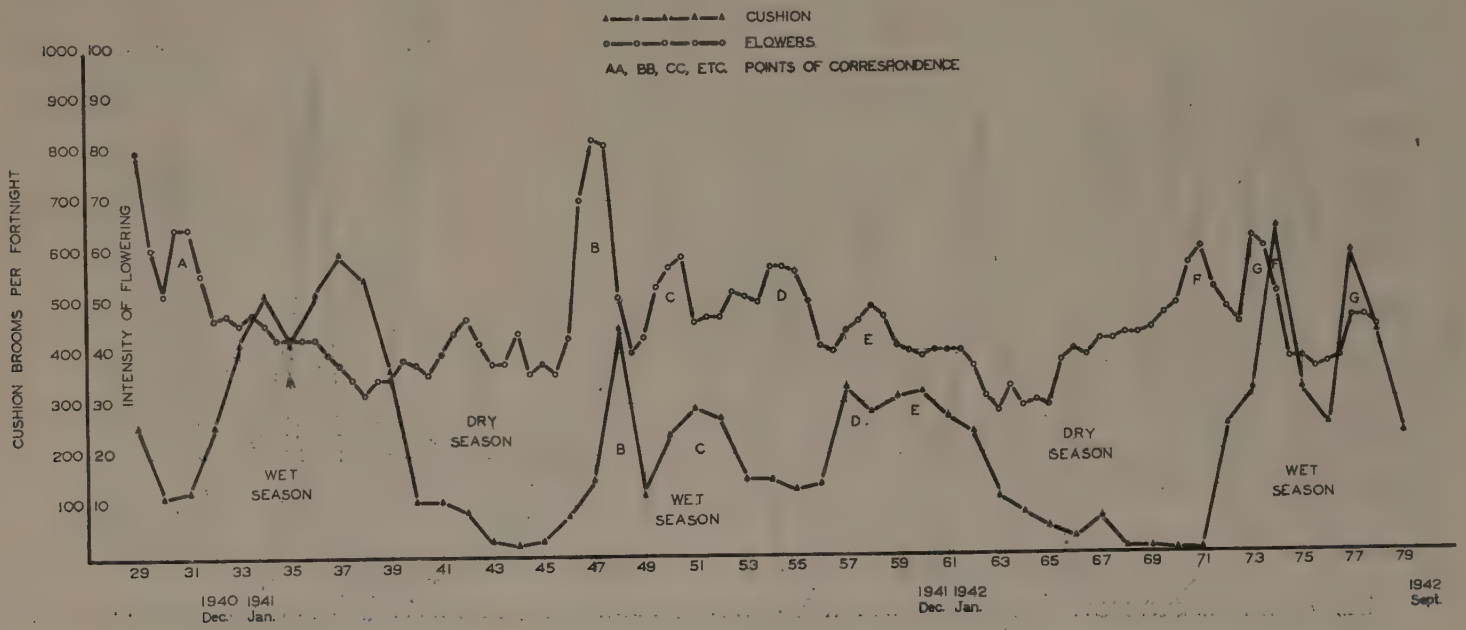

FAN BROOMS AND FLUSH
FAN BROOMS
FLUSH
BROOMS PER FORTNIGHT
ESTIMATION OF FLUSH
1200 240
1100 220
1000 200
900 180
800 160
700 140
600 120
500 100
400 80
300 60
200
100 20
DRY SEASON
WET SEASON
DRY SEASON
WET SEASON
38 40 42 44 46 48 50 52 54 56 58 60 62 64 66 68 70 72 74 76 78 80
1941 Feb.
1941 1942 Dec. Jan.
1942 Sept.

FIGURE VI

CUSHION BROOMS AND FLOWERS



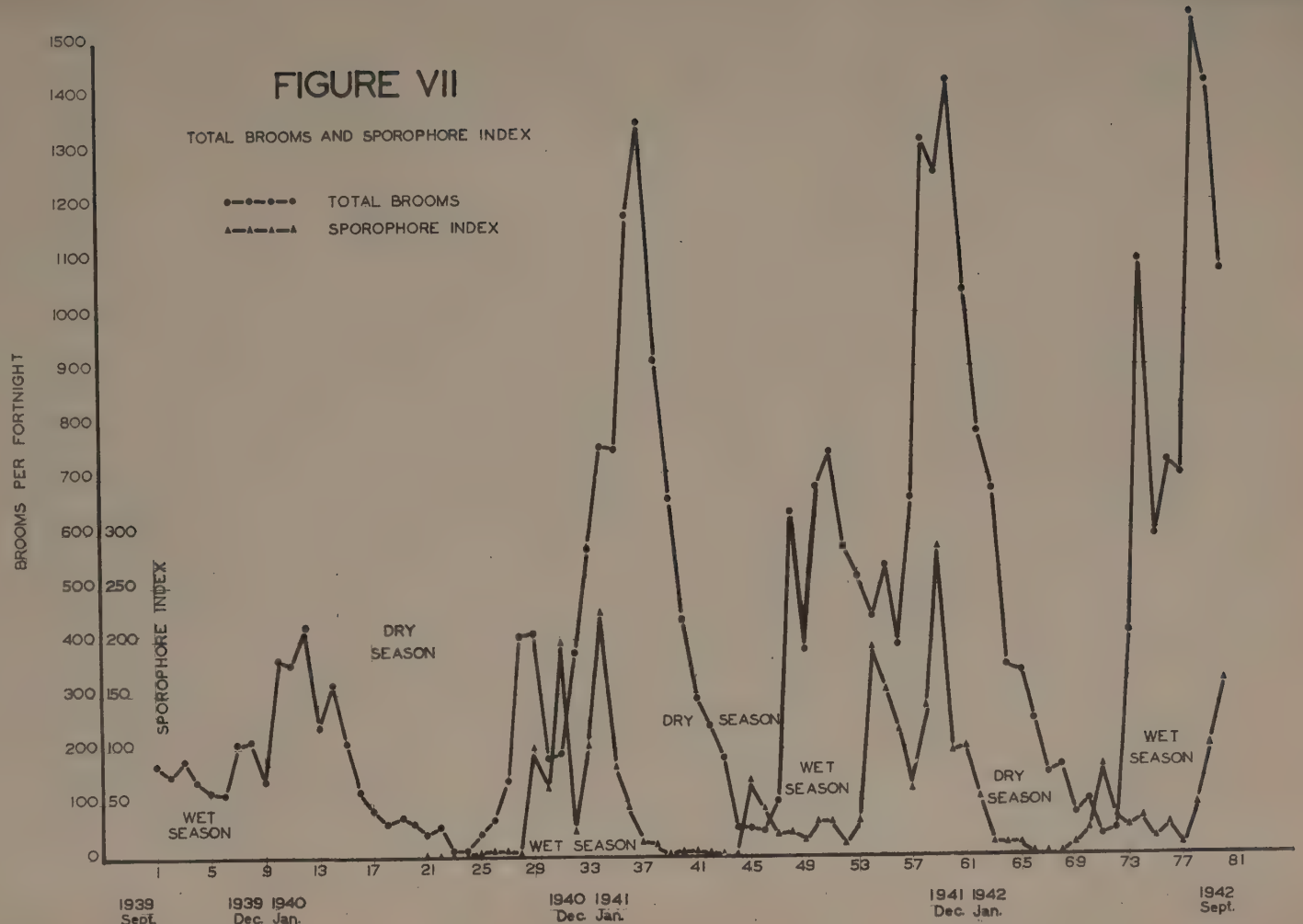


FIGURE VII
TOTAL BROOMS AND SPOROPHORE INDEX
TOTAL BROOMS
SPOROPHORE INDEX
BROOMS PER FORTNIGHT
SPOROPHORE INDEX
1500
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
300
250
200
150
100
50
DRY SEASON
WET SEASON
WET SEASON
DRY SEASON
WET SEASON
DRY SEASON
WET SEASON
1 5 9 13 17 21 25 29 33 37 41 45 49 53 57 61 65 69 73 77 81
1939 Sept.
1939 1940 Dec. Jan.
1940 1941 Dec. Jan.
1941 1942 Dec. Jan.
1942 Sept.

IV. –Flushing and Fan Broom Formation

Cacao changes its leaves frequently, but at no time is a healthy tree entirely without leaves. Flushes of new leaves occur at fairly regular intervals and a healthy tree may be expected to produce five or six flushes in a year. Leaves belonging to two or even three consecutive flushes can usually be found on a tree at the same time. Over fairly wide areas trees tend to produce new leaves at the same time. Young trees tend to flush more frequently than older trees.

Pyke (12) in 1932 studied periodicity of flushing on old trees and found that peaks occurred at fairly constant intervals of from 60 to 95 days giving four or five flushes per annum. The first occurred at the beginning of the rains in June; the second about 85 days later in August-September; one or more smaller flushes occurred at the end of the wet season, and there was a vigorous flush early in the dry season in February-March.

McKee (8) working with young trees about 3 to 4 years old noted six to eight flushes a year at intervals of 50 to 60 days. These became somewhat irregular during the dry season, as young cacao tends to flush less regularly than older trees.

Humphries (7) working with old trees on River Estate found four or five main flushes a year. These consisted of a big flush in May-June, followed by a less intense flush in September-October; during the first year there was no further flushing until January, but the second year there was a light flush in November-December. The January-February flush on both occasions was followed by a lighter flush about 7 weeks later, making a total of four or five for the year.

A matter of great interest of which the significance is not yet fully realised is the close relationship which Humphries (7A) finds between flushing and maximum temperature. Flushes tend to occur at a time when daily maximum temperatures are high, an observation which may be of considerable value when the climatic relationships of witches' broom disease are investigated.

The 8 to 10 year old trees used during these investigations flushed somewhat irregularly about six times a year at intervals of 50 to 100 days (Fig. V). In 1941 the first flush occurred in January-February and was followed at short intervals of 35 to 50 days by three more flushes. The first two occurred during a very severe drought and were quickly shed, but the third (the fourth flush for the year) which came at the same time as the first rains held on longer. The next flush of about the same intensity occurred in August and was followed by lesser flushes in October and December-January making 6 or 7 for the year of which the two occurring in the March-May drought were definitely unusual. In 1942 the December-January flush was followed by a small flush in March and

a very intense flush after the early rains in May. Subsequent flushes occurred in July, October and December, making six for the year. This probably represents a more usual picture of a year's flushing than was seen in 1941.

There is an indication that the first flush of the wet season is the heaviest and most general, and that succeeding flushes are lighter and less universal. A knowledge of this phenomenon is necessary before the formation of fan brooms on cacao trees can be understood.

It has already been shown by inoculation experiments (3) that only young tissues can be infected and therefore young flush is necessary for infection. Montserin (10), Briton-Jones and Cheesman (6) and more recently Baker and Crowdy (3) consistently failed to infect the dormant buds. The developing bud on which the stipules have opened and the young leaves are visible, and less than one and a half inches long, is most susceptible. Therefore, for infection to take place, young flush must be present. After infection the young flush hardens normally for a period varying from three weeks to over three months, and the first visible symptom of a developing broom is usually the swollen pulvinus of the subtending leaf. At this stage the bud may be a little larger than normal but nothing further will happen until the tree starts to flush again. When this happens these ' B4 ' brooms may begin to grow into the larger and better known types. If the shoot on which an infection has become established misses the next flush (and by no means every twig develops new leaves each flush) it may dry up and fail to develop any further. There is therefore in this disease a long incubation period of 3 weeks to 3 months between infection and the development of a fan broom. True latent infections of the *Colletotrichum gloeosporioides* type described by Baker and Wardlaw (5) do not occur.

Therefore brooms which develop with one flush must have been initiated during the previous flush and the fact that the sporophore index is positively correlated ($r = +0.47^{**}$) with broom formation five weeks later is additional evidence that this explanation is correct.

An appreciation of these facts explains several hitherto puzzling aspects of the disease. It is now obvious that there can be no high correlation between fan brooms and the current flush figures. The low positive correlation found ($r = +0.31^{**}$) is due simply to the fact that, assuming infection to be constant, more brooms will develop when trees are flushing than when they are not. It has also been noted that the heavy flush occurring near the beginning of the dry season, usually in February, contains many brooms although by this time sporophore production has fallen considerably and conditions are probably too dry for infection. The explanation of this is that the infections which caused these brooms occurred during the previous December when sporophores were plentiful and conditions suitable for infection. Similarly the first

flush of the wet season occurs at a time when sporophores are plentiful and conditions apparently suitable for infection yet contains very few brooms. The reason for this is that the previous flush took place during dry weather when sporophores were very rare and environmental conditions unsuitable for infection. The maximum development of brooms which comes with the January-February flush is explained by the favourable conditions at the time of the last preceding flush in November which is normally a cool and very wet month in Trinidad and by the fact that the sporophore index is then (November) very high.

As far as fan broom production is concerned therefore, once the long incubation period is appreciated, the life history of the disease presents no difficulties.

V.—Flowering and Cushion Broom Formation

Cacao trees flower almost all the year round, but flowers are more numerous at certain seasons. Increases in flowering correspond roughly with the main vegetative flushes (*see* Figs. V and VI) and production is greatest towards the beginning of the wet season. Successful cushion inoculations resulting in the formation of all types of cushion broom have recently been completed by Trueblood (20) and McKee (9) on whose results much of this discussion is based.

Cushion broom formation is strongly correlated (1940-41 r= +0.57, 1941-42 r= +0.77) with the flower production of a tree, indicating that the larger and more numerous the cushions are and the longer they remain active the greater will be the number of cushion brooms formed on that tree during the year. The incubation period between infection and the first visible signs of a cushion broom is about 4 weeks. It is obvious therefore that for use in an area infested by witches' broom disease very freely flowering trees are highly unsuitable. (Cacao trees normally produce many flowers which do not set fruit ; certain trees, and especially those which are self-incompatible, produce a great excess of flowers at certain seasons).

Cushion brooms develop slowly after infection. The first sign is usually one flower which fails to abscise or has a slightly thickened pedicel. Several weeks may elapse from this stage until the cushion reaches the stage of producing nothing but diseased flowers or thickened vegetative shoots and finally dies. Recent inoculation experiments have shown that once a cushion is infected it will go on producing diseased flowers and shoots for four or five months as the infection penetrates deeper and deeper before it eventually dies. This is in contrast to the vegetative broom which develops rapidly and dries up in six or eight weeks. Recovery is also possible but only from the early stages. In the early stages if the infected flower and its pedicel are removed the cushion will often become normal again and produce no more diseased flowers ;

also, occasionally, if a more advanced cushion broom is cut flush with the surface of the bark it will recover and its more deeply embedded tissues will produce healthy flowers. This is taken as evidence that a cushion infection occurs on the very young developing tissues which hypertrophy rapidly as they develop, while the spread of the infection to the more deeply seated parts of the cushion is much slower. There is no evidence that the infection from one cushion can spread through the bark of the tree and infect neighbouring cushions. In control, therefore, infected cushions should be cut flush with the surface of the tree and no attempt should be made to excise them.

VI.—Pod Infection

All types of diseased pods have now been produced by artificial inoculation. This work was carried out by R. K. McKee, a short account of whose work follows. A more detailed account of his investigations has been published (9).

Marasmius perniciosus can infect the reproductive system of the cacao tree causing a variety of malformations and diseased tissues. These have been briefly described and illustrated (3) but some further notes on the types of infection are given here, on account of their bearing on the inoculation experiments to be described.

Infections of the reproductive system may be conveniently divided into those involving pods and young cherelles and those resulting from diseased cushions and diseased flowers. Pod infection has been further classified by Stahel (14) as follows :—

1. Directly infected pods (*a*) swollen pods.
   (*b*) indurated pods.
2. Indirectly infected pods.

Swollen pods are those in which there is one or more hypertrophied area where the mycelium of the fungus can be found ramifying in the intercellular spaces of the host tissues. Such pods do not reach maturity and the host tissues die, the breakdown spreading outwards from the infected area. If natural wilting of the cherelle occurs before the breakdown stage is reached, the infected areas remain alive and turgid for some time after the death of the surrounding tissues, giving a characteristic and easily recognised appearance.

In the indurated pods infection does not produce any visible hypertrophy, the pod reaching maturity before internal breakdown occurs, unless it wilts naturally when the infected areas remain alive longer than those which are free of the mycelium. At maturity, a localised brown or blackened area develops on the surface, and on opening the pod it is found that this necrosis extends over a considerable

part of the pod and that the majority of the beans are useless. Such pods are usually hard and abnormally woody in the infected area, hence the name " indurated pods."

A third type of infected pod is commonly found which may be considered as intermediate between the above types. Here there is no marked hypertrophy, but the pod stalk and shoulders are rather larger than the normal and the pods tend to be straight-sided rather than curved resulting in a characteristic ' carrot shape '. Such pods do not reach maturity : for when they are half or three quarters grown a general necrosis takes place. The first sign of necrosis is the breakdown of the vascular strands which give a stippled appearance to the ground tissue. This leads rapidly to the complete destruction of the pod which becomes a uniform brown in colour.

Thus the fungus mycelium for some time after infection lives in the intercellular spaces of the pod, which may or may not develop a visible hypertrophy. Such tissues will wilt more slowly than the uninfected areas. As the pod reaches maturity necrosis sets in starting from the diseased areas and the fungus soon spreads saprophytically through the whole pod.

Cushion infection may result in either diseased flowers (the ' star ' blooms) or infected vegetative shoots, often of large size. Infected pods (the indirectly infected pods of Stahel's classification) are also produced from diseased cushions. These are very distorted in shape and do not produce any beans. They are usually considered to be developed parthenocarpically from diseased flowers and unpublished work by Posnette indicates that this explanation is correct. Such cherelles are not of common occurrence and cannot be considered as having any great practical importance.

When infection is severe the direct losses due to pod infection under field conditions can be very serious. A survey of a severely infected plot at River Estate shows that in some months as much as 75 per cent. of the pods were destroyed by witches' broom disease ; and since other pod-rots also occurred, a negligible quantity of healthy ripe pods was harvested as compared with previous years when the disease was less prevalent (Table VI).

Prior to this work the only successful inoculations of pods were made by Stahel (14) who obtained 39 diseased pods, or about 60 per cent. of the inoculated cherelles which reached maturity. He concluded that swollen pods were formed only if the cherelle is infected when less than 20 mms. long, while indurated pods are formed from larger cherelles. If the fruit is more than half grown before infection he states that the shell only is affected, the beans being unharmed. With the exception of 5 successful inoculations there is no published record of the inoculation of cushions, although Trueblood (20) obtained four diseased cushions from a total of 140 inoculated.

TABLE VI

Pods Harvested—River Estate

Field 19. Observation plot of 76 trees

Date	Total pods	Healthy pods	W.B.D. pods	Other diseases pods	% W.B.D. pods
13-1-42	127*	61	38	28	30
17-2-42	115	32	37	46	32
3-3-42	38	21	15	2	39
5-5-42	271	159	8	104	3
7-7-42	760	616	29	115	4
8-9-42	18	16	0	2	0
24-11-42	348†	22	212	114	61
8-12-42	85	1	44	40	52
21-12-42	124	5	84	35	68
5- 1-42	87	7	43	37	49
19- 1-42	104	11	82	11	80
2- 2-43	85	15	63	7	74
16- 2-43	91	10	69	12	76
2- 3-43	76	0	56	20	73
16- 3-43	149	11	71	67‡	48
29- 3-43	171	13	43	115‡	25
13- 4-43	89	12	15	62‡	17
27- 4-43	79	23	16	40‡	20
Totals	2817	1035	925	857	33

* full size pods only

† all pods longer than 7.5 cms.

‡ increase due to dry season wilt

A series of inoculation experiments on both cushions and young cherelles was started in July 1942 using the same method as that employed by Baker and Crowdy (3) in their successful inoculations of vegetative tissues. A spore suspension is applied with an atomiser, inoculations being made as early at night as a suitable spore deposit can be obtained. By this method considerable numbers of both cushions and young cherelles have been successfully inoculated. Diseased cushions can be detected by the characteristic malformations, while with pods any doubtful cases were confirmed either by isolation of the fungus or by microscopic examination of the mycelium in the tissues.

Of a total of 600 cherelles and pods inoculated some 10 per cent. have been successful but, since about 300 wilted before sufficient time had elapsed for the symptoms to become visible, the percentage of successful inoculations was presumably near 20 per cent. There was a

considerable variation in the percentage of successful inoculations from tree to tree and also on the same tree on different occasions. Individual experiments have given as much as 42 per cent. of the inoculated cherelles infected.

All the types of diseased pods found in the field have been reproduced by artificial inoculation, the swollen and distorted type being the most common. Symptoms may appear in just over three weeks or may not show up for three months, in cases where no distortion occurs. No cherelles of over 6 cms. in length when inoculated have been infected, even in an experiment where 53 per cent. of the cherelles below that length were infected (Table VII).

Two hundred and sixty-three cushions were inoculated of which 60 became infected. Of these, 35 per cent. sooner or later produced vegetative shoots, the majority being formed either within a few weeks after inoculation or alternatively a considerable time after the first diseased flowers were noted. This suggests that in these latter cases the base of the cushion becomes infected by mycelium spreading back from diseased flowers rather than directly by spores. The remaining 65 per cent. of the infected cushions produced diseased flowers, all the different

TABLE VII

Pod inoculation at I.C.T.A.

Cherelle length in cms.	Number inoculated	Number successful	% success
FIELD 1			
0-0.9	57	12	21
1-1.9	86	28	33
2-2.9	60	17	28
3-3.9	17	4	24
4-4.9	14	5	36
5-5.9	4	2	(50)
6-6.9	1	0	(0)
7 and over	8	0	0
FIELD 2			
0-0.9	—	—	—
1-1.9	4	2	(50)
2-2.9	9	5	56
3-3.9	18	16	89
4-4.9	9	7	78
5-5.9	3	3	(100)
6-6.9	2	1	(50)
7 and over	12	0	0
Totals	304	102	33

types of infection found in the field being reproduced. In two cases typical 'indirectly infected pods' were found on a diseased cushion.

A more detailed account of these experiments and of others which are still in progress will be published elsewhere (9).

VII. –Resistance

Stahel, Stell and Pound are all confident that immune or resistant cacao trees exist in South America. Stahel (1915) noted differences in susceptibility in Suriname, Stell (17) visited Ecuador and saw trees which he considered to be resistant, and Pound (11) has made extensive travels in South America and has collected pods from trees in the Amazon basin which he considers to be immune or resistant to the disease. This material is now being propagated in Trinidad. Since very few seedlings taken from a resistant or immune tree of a heterozygous crop like cacao are likely to show the resistance of the parent tree, Pound has recently returned to South America to obtain material for vegetative propagation from these same trees.

Differences in susceptibility are also known to exist in Trinidad and in 1934, 150,000 trees were surveyed by the Trinidad Department of Agriculture and in 1936 all but 12 had been eliminated as susceptible. Budded clones and open pollinated seedling progeny of these trees are now established at Marper estate. Some of this material apparently shows resistance when compared with seedling plantation cacao.

In addition work at River Estate (1) has shown that in a plot of only 76 trees, all having the same female parent, considerable differences in susceptibility exist. Considerable differences in susceptibility are also becoming apparent between the clonal plantings of I.C. selections on this estate. It would appear therefore that the existence of resistant types both in Trinidad and in South America is proved beyond any reasonable doubt.

Evidence such as has just been outlined above would be expected if resistance was due to a large number of genes of small individual effect occurring at random in the unselected population. Selection acts as a sieve, separating out the trees which by chance carry a considerable number of these resistant genes. The area in South America where resistance is most common is the area where the disease has existed longest (or is indigenous), hence natural selection for resistance has operated there for a considerable period. For this reason whether or not resistance mechanisms differ in Trinidad and the Amazon it is to be expected that resistant trees would be more common or more highly resistant in the Amazon Valley than elsewhere.

The mechanism of resistance to witches' broom disease is at present entirely unknown. Resistant trees, as known in Trinidad, are those which produce a smaller number of fully developed brooms; not smaller,

malformed or poorly developed brooms. Results from River Estate and elsewhere indicate that although there is probably no immunity to the disease in Trinidad cacao, great differences in susceptibility exist, especially when fan brooms alone are considered. Cushion broom formation is strongly and positively correlated with flower production, and the incidence of diseased pods is not positively correlated with fan broom production. This evidence, though admittedly incomplete at present, indicates firstly that there may be no inherent physiological resistance to the disease in Trinidad cacao, and secondly that resistance may be a matter of disease avoidance by certain trees.

The important problem from the Trinidad cacao growers' point of view is whether an immune or sufficiently resistant type of cacao which will be a good yielder and of a sufficiently high quality to be acceptable commercially can be found in Trinidad or South America and then vegetatively propagated for use in areas where the disease is severe. If no such strain can be found it is likely that these areas will have to be abandoned, as hybridisation calculated to introduce the resistance of a poor type of South American cacao into high quality Trinidad cacao may be ruled out because results will come too late to save the industry. Practically nothing is known at present of the genetics of cacao and adequate knowledge of this subject can only be obtained by many years' research. Until such knowledge is available breeding work can only be of the hit or miss type done almost entirely in the dark, whatever is done it will be very many years before results of any commercial value can be expected.

A similar problem exists in Ecuador where the position is made worse by *Monilia* disease. Only the propagation of varieties resistant to these diseases is likely to save their cacao industry.

For climatic reasons it is likely that in many parts of Trinidad the disease will remain relatively mild and that it will be possible in these districts to grow high quality susceptible strains such as some of the I.C. selections with success.

VIII. –Control Measures

There are at least four main methods by which the control of the disease could be attempted : firstly by spraying or dusting, secondly by the removal of brooms, thirdly by modifications in agricultural or horticultural methods, and fourthly by the use of immune or resistant varieties of cacao.

It would appear that spraying or dusting can be ruled out right away as unsatisfactory and uneconomic. When the disease was first investigated in Suriname, Stahel (1915), following up the unpublished work of ter Laag, recommended spraying the trees with 2 per cent. Bordeaux mixture once or twice a year. He also stated that to profit

fully from the spraying it was necessary to remove brooms from the trees once every 2 to 4 *weeks*. One spraying was to be applied in the main dry season, the other in the little dry season. Later Stahel (1919) concluded that if brooms were removed every 3 to 4 weeks spraying was unnecessary. In 1928 Stell (15) recommended the use of a Bordeaux mixture spray in Trinidad, but experiments conducted subsequently by the Department of Agriculture yielded only negative results. More recently a second series of experiments made by Thorold (unpublished work) at River Estate gave a similar result.

Owing to the rough nature of the ground on many Trinidad cacao estates, the height of the trees, and difficulties in water supply, spraying would always be expensive, and dusting, though easier and cheaper, is probably less effective. Because of the high cost of the operation therefore, it is likely that spraying would prove uneconomic even if a high degree of control was possible and the experiments certainly do not indicate that this high level of control is likely to be attained.

The second method of control, the removal of brooms, at first sight appears more promising. In theory, if all the brooms over a large area could be removed before they produced sporophores the disease would not only be controlled but could be brought to a very low level and almost eliminated. Complete elimination might prove impossible owing to the ability of the fungus to lead a saprophytic existence for a considerable period. In practice this is not possible and the success or failure of the method depends on the following points.

Firstly, how many times a year must brooms be removed? Stahel (1915) suggested every 3 to 4 weeks or a minimum of twelve times a year. Stell (16) having evidence that brooms do not normally produce sporophores in less than 12 weeks suggested four times a year with 'Special Campaigns' in May and October, and Baker and Crowdy (3) recently suggested that two clearances per annum should be sufficient. However, in Trinidad with expensive and inefficient labour it is doubtful if even two effective rounds a year could be completed sufficiently cheaply in areas where the disease is severe. A cost of $25.00 per acre per annum would probably be exceeded at the present day for heavily diseased cacao, and this represents approximately the value of 200 lb. of cacao at $12.50 per cwt. The average yield of cacao in Trinidad is only about 200 lb. per acre so that it is obvious that this treatment could only prove economic on either high yielding fields or on lightly infected cacao where the cost per acre would be much lower.

Secondly, if only two clearances are to be made in a year, when are the most favourable times? It is obviously waste of time to remove brooms when they are developing rapidly; for a few weeks after an estate has been 'cleared' it will be heavily reinfested. The most favourable period is therefore in April and May when infection and broom

formation are at a minimum. It has been shown (3) that if a thorough clearance was made at that time, sporophore formation and therefore infection, would be prevented until the beginning of October. September and October therefore, when there is often a 'little dry season' and some reduction in broom formation, are selected for the second cutting. If that cutting was efficiently carried out, sporophore formation in December and January, the most dangerous period of the year, when climatic conditions appear especially favourable for infection, would be largely prevented. We would go further and suggest that, provided these two cuttings were efficiently done, the removal of brooms at other times of the year would be a waste of time and money.

Thirdly, is it possible to remove sufficient brooms from the trees to control the disease, and is it necessary to remove all types of broom? In the previous memoir of this series (3) Baker and Crowdy concluded that while medium-sized and large brooms constituted a dangerous source of infection, the smaller brooms (C3, A1 and B4) which were under two inches in length produced relatively very few sporophores. Furthermore it was doubtful if the time expended in searching for them was adequately repaid by the reduction effected. There was, however, a risk that small brooms might eventually grow into large brooms and that until it could be justified by field experimentation a systematic policy of neglecting the smaller brooms could not be recommended. But even assuming that it is only necessary to remove the larger brooms, experience shows that skilful labourers, who have known the diseaes for years, leave many behind. Work with a ladder has shown how often several large brooms invisible from the ground may be left in the top of a tree. Considerable difficulty is experienced in dealing with old trees where the canopy is high and interlacing and the use of ladders would slow down the work considerably and increase its cost. The destruction of brooms by burying or burning is probably unnecessary as provided they are not supported on branches or piled into heaps, they very seldom produce sporophores and soon decay or become overgrown with weeds.

Fourthly, can the disease be successfully controlled on an estate which is surrounded by other properties which are abandoned or on which the disease is uncontrolled? Experiments carried out by the Department of Agriculture at Marper Estate (18) suggested that pod losses could be kept under 5 per cent. in spite of the disease being uncontrolled on contiguous properties. This was corroborated by observations at River Estate (4) which indicated that the *more serious* spread of spores from an infested area might be over as short a distance as 200 yards.

Important experiments to test this method of control were started by the Department of Agriculture in 1941, the results of which have been published by Thorold (19). The results of two years' work carried out under difficult conditions are however very disappointing and indicate that even in a block of over fifty acres of cacao a satisfactory control could not be obtained in this way.

We must conclude therefore that although in the early days of the disease this method of control seemed likely to succeed, at present, in the light of recent experiments and because of the increased cost of labour, it appears to be useless unless it can be carried out simultaneously and efficiently over very considerable areas (at least of the order of 250 acres) or on well isolated areas. Even in such circumstances its success is very far from certain, but the general deduction from the experiments and from experience of this method of control in recent years at least leaves it possible that control might be feasible in these conditions. It is probably only worth considering for fields of young high-bearing trees remote from old infested cacao fields which constitute reservoirs of infection.

Control of the disease by agricultural or horticultural methods has been considered, and van Hall and Drost (21) introduced the so-called pollarding method in 1907. The trees were cut right back to primary branches and a full year's crop was lost. Weak trees often died, especially if subjected to drought after pollarding. Stahel (1915) concluded that the removal of brooms was preferable to this drastic cutting of the trees. Briton-Jones and Cheesman (6) suggested that the trees should be pruned and shaped at the same time as the brooms are removed and that if the trees were severely infested they could be heavily cut back with advantage. Time and money can be saved by combining the two operations in this way. It is customary on Trinidad cacao estates to trim the trees once a year in the dry season (although apart from shaping the trees it is not obvious that this 'pruning' has any value). This operation can be made to coincide with the April-May removal of brooms. This is however little more than a modification of the previously discussed method of control by removal of brooms and would undoubtedly be the best method to use in the rehabilitation of seriously diseased or abandoned cacao. The piecemeal removal of a thousand or so brooms from a heavily diseased tree in the end produces a similar though less satisfactory result at the expense of more time and money.

With the exception of closer planting other modifications of existing horticultural methods although much discussed have not been tested experimentally and appear to offer little likelihood of affording a successful control method. The same is almost certainly true of any alteration in manuring. Many people, and especially those with West African experience, believe that 8 or 9 feet is a better planting interval

for cacao than 12 or 14 feet, and that if planted in this way the trees would flush less often and suffer less from fan brooms. Furthermore, the heavy canopy might to some extent protect the pods from infection. While this has not been proved experimentally, the close planted blocks at River Estate do appear to suffer less from the disease than those on which the trees are more widely spaced.

It therefore appears probable that the control of the disease by the removal of brooms is at present impossible. That being so, the best hope of controlling the disease is by the use of an immune or resistant variety of cacao, and work on these lines is of the utmost importance. It is shown in this paper that differences in varietal susceptibility exist in the relatively small population of 76 cacao trees investigated. A survey of 150,000 cacao trees carried out by the Trinidad Department of Agriculture in their search for a resistant variety of cacao yielded clones which although not immune, may be of the greatest interest and value. Most important of all are the immune or resistant varieties of cacao, which have been collected in South America by Pound (11). What degree of resistance exists in South American cacao, or even whether there may be complete immunity to the disease is at present unknown ; but Stahel, Stell and Pound are all confident that resistant material will be found. Observations on South American material grown in Trinidad are not yet sufficiently advanced to make any statement except that the plants show promise. Whether the resistant types when found will produce an economic yield of commercially saleable cacao is not by any means certain but if they failed to do so and a hybridisation programme was suggested with a view to introducing the resistance of South American strains into high quality Trinidad cacao, the production of planting material on a commercial scale would be relegated to the dim and distant future. A relatively high yielding strain, even although it produced small and dark-coloured beans, would be of considerable value. Even assuming that an immune and commercially satisfactory variety exists in the Amazon material, *at least* 15 or 20 years must elapse before it can be planted sufficiently widely to improve the condition of the heavily diseased areas of Trinidad.

To summarise our knowledge of control methods therefore, it cannot be said that the position is at present at all promising or even hopeful for some years to come. Spraying and dusting can be ruled out as ineffective and uneconomic. Modifications in agricultural methods do not appear feasible at present and anyhow would require detailed field experiments before they could be recommended for general use. The removal of brooms appears not only to be too difficult and expensive, but even to be ineffective. We are left then with the unsatisfactory conclusion that for the present the direct control of the disease is impossible economically and that the use of an immune or sufficiently

resistant variety of cacao of which the existence is not so far finally established, is the only possible method of controlling the disease. Future work should therefore be concentrated on this aspect of the problem and on a study of the disease in relation to climatic factors in order to ascertain in what areas the disease is likely to be sufficiently serious to render the cultivation of susceptible varieties of cacao unprofitable.

IX.—Summary

1. The results of three years study of a plot of 76 trees at River Estate are discussed. Considerable tree to tree variation, indicating differences in susceptibility, were found.

2. There is a marked seasonal variation in broom formation with a maximum in January or February and a minimum about June or July.

3. Cacao trees flush about five or six times a year at intervals of 60 to 90 days and brooms appear with the flush. The total amount which a tree flushes during the year has, however, little effect on its fan broom production.

4. Cacao trees flower all the year round, but more strongly at certain seasons than others. Flowering and cushion broom formation are strongly and positively correlated.

5. The different types of diseased pods and their artificial production by inoculation are described. Only small pods less than 6 cms. long could be infected with the disease.

6. The resistance or susceptibility of Trinidad and South American cacao to the disease is discussed and it is concluded that in the Trinidad material some degree of resistance undoubtedly exists. Strains of South American cacao presumed to be highly resistant, are at present under observation.

7. Control methods are discussed and it is concluded that in areas where the disease is severe, all the known methods are either ineffective or uneconomic, and that probably the only solution to the problem lies in the discovery of a resistant variety of cacao.

X.—Acknowledgments

We are indebted to the Trinidad Department of Agriculture for much help during the course of this investigation; especially to Mr. R. O'Connor, Manager of River Estate, and Mr. C. A. Thorold for helpful advice and permission to use his unpublished results. Much of the field work was carried out by Messrs. R. K. McKee, T. B. Cooper, D. Westwood and A. C. Trueblood, post-graduate students in plant pathology at the Imperial College.

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Copies of this Memoir may be obtained on application
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TRINIDAD:
Printed by the Government Printer,
Government Printing Office,
Port-of-Spain.

1944